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ASSESSING THE REWARDING ASPECTS OF A STIMULUS ASSOCIATED WITH EXTINCTION THROUGH THE OBSERVING RESPONSE PARADIGM

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ABSTRACT: Two experiments determined the role that a stimulus associated with extinction plays in the maintenance of the observing response in goldfish. In Experiment 1, goldfish were trained to respond on either a mixed or a multiple schedule of reinforcement. By swimming through a light beam at the opposite end of the tank, one group of fish could produce stimuli associated with food (S+) and extinction (S-). In a second group, fish could terminate presentations of S+ and S-. For both groups, reward was response independent. S+ appeared to maintain the observing response, whereas S- played an aversive role. In Experiment 2, goldfish were trained to respond on a multiple schedule of reinforcement. Reward was response dependent. Goldfish terminated S+ at a significantly lower rate than S-. The two experiments together show that S- will not support observing even under conditions where response efficiency could be improved by observing. Results are discussed in light of theories of the observing response based on secondary reinforcement, information, and energy savings.

INTRODUCTION

Wyckoff (1952, 1969) showed that pigeons will learn to press a treadle that does not affect reinforcement availability but does provide a cue that predicts periods of reinforcement (S+) and extinction (S-). The finding that animals will work for such a cue, i.e., make observing responses, has been replicated numerous times and with a variety of species including goldfish (Purdy & Peel, 1988), pigeons (Blanchard, 1975; Browne and Dinsmoor, 1974; Mulvaney, Dinsmoor, Jwaideh, & Hughes, 1974), rats (Daly, 1985; Prokasy, 1956), rhesus monkeys

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(Lieberman, 1972; Steiner, 1967), and humans (Fantino & Case, 1983; Perone & Baron, 1980).

Several explanations have been proposed to account for the data. First, Wyckoff (1952) maintained that S+ reinforces observing through secondary, or conditioned, reinforcement and that S- punishes the response through secondary punishment. On balance, the rewarding properties of S+ outweigh the punishing properties of S-, and observing persists. In a refinement, Fantino (1977) stated that the strength of a stimulus to act as a reinforcer is determined by two factors. In factor one, a stimulus acquires secondary reinforcement value by being associated with a reduction in time of delay to reward relative to a second stimulus. Thus, a stimulus correlated with a greater reduction in time to food presentation will be a stronger reinforcer than one correlated with a lesser reduction in time to food. Stimuli not correlated with reductions in time to food should not serve as reinforcers. A second factor influencing secondary reinforcement value concerns the relative reduction in time to reward as measured from the previous reward. Thus a stimulus that predicts reward after a short delay in a schedule where overall reward density is low will be a stronger secondary reinforcer than that same stimulus would be if reward density were increased.

The uncertainty reduction hypothesis provided a second explanation for observing behavior. Berlyne (1957) and Hendry (1969) argued that observing was reinforced through the reduction of uncertainty. Uncertainty was viewed as an aversive stimulus, and observing persisted because it reduced uncertainty about forthcoming events. Both information theorists and secondary-reinforcement theorists contend that S+ is rewarding, but the two groups differ with respect to their treatment of S-. Conditioned reinforcement theorists contend that S- is either neutral or punishing whereas information theorists argue that S- is always rewarding since it reduces uncertainty. The evidence supports secondary-reinforcement theory (e.g., Blanchard, 1975; Browne & Dinsmoor, 1974; Dinsmoor, Browne, & Lawrence, 1972; Mulvaney, et al., 1974). In each of these studies, S+ strengthened observing behavior and S- suppressed it.

A third explanation of observing has received less attention in the literature. This explanation suggests that organisms may observe to improve response efficiency. Thus animals may observe because they can respond maximally during food segments and stop responding during extinction. The argument that an animal may observe in order to maximize energy intake and minimize energy output relates to theoretical positions concerning optimal foraging (Kamil & Sargent, 1981; Kamil, Krebs, & Pulliam, 1987; Shettleworth, 1988). In

observing paradigms, to maximize energy input and minimize energy output, the animal must take advantage of information correlated with periods of food availability and extinction by confining its responses to those conditions where food is available. In this argument S+ is rewarding in that it allows the animal to maximize energy input, and S- provides a source of reward because it can be used to conserve energy. However, unlike the uncertainty reduction hypothesis, which states that S- should always be rewarding, the effort argument contends that S- should be rewarding only in those instances where reward is response-dependent and where the instrumental response is effortful. In studies involving humans (Case, Fantino, & Wixted, 1985; Case Ploog, & Fantino, 1990; Fantino & Case, 1983; Perone & Baron, 1980) and in studies involving rhesus monkeys (Lieberman, 1972; and Steiner, 1967) precisely these results have been obtained. Presentation of S- was rewarding only in those instances where response efficiency could be improved.

Interestingly, the effort argument has received no support in the pigeon literature. In no instance has it been shown unambiguously that S- is rewarding in those cases where response efficiency could be improved (Dinsmoor, Browne, & Lawrence, 1972; Mulvaney, Dinsmoor, Jwaideh, & Hughes, 1974; Dinsmoor, Bowe, Green, and Hanson, 1988). That S- will support observing in primates but not other species when its presentation can lead to an improvement in response efficiency suggests the possibility of species differences. It may be that primates are capable of developing a strategy of responding that can lead to an improvement of response efficiency, whereas pigeons are not.

One method to determine whether different mechanisms may be supporting the observing response for different species is to examine these variables in very different organisms. This strategy was utilized by Bitterman (1975) who argued that "comparisons of distantly related animals . . . provide a much broader picture of the evolution of behavior." (p. 704). It is likely that species that are considered cognitively less complex are not capable of developing a strategy of responding that leads to an improvement in response efficiency. For these animals, conditioned reinforcement, in its purest sense, may be the sole mechanism that supports observing.

Fish have been shown to be capable of stimulus-response learning, but they have not been shown to be capable of stimulus-stimulus learning, (Bitterman, 1975). In a spaced-trials procedure, goldfish do not show negative contrast (Lowes & Bitterman, 1967), the magnitude of reinforcement-extinction effect (Gonzalez, Potts, Pitcoff, & Bitterman, 1972), or the partial reinforcement-extinction effect (Gonzalez & Bitterman, 1969). Since fish apparently form only stimulus-response

bonds, conditioned reinforcement may be the only mechanism supporting observing in fish. This would suggest that for a fish, a stimulus associated with extinction would not be rewarding even though it could be associated with an increase in response efficiency. The present experiments tested this hypothesis.

EXPERIMENT 1

METHODS

Subjects

Twelve goldfish (*Carassius auratus*), 8 - 12 cm in total length, obtained from the B and P Minnow Farm, Milano, TX served as subjects. All were experimentally naive but were adapted to laboratory life. Subjects were housed individually in compartments within a large tank and fed only during the experimental procedures. Polyester batting and charcoal filtered the water in the closed water system.

Apparatus

A long Plexiglas tank (107 x 15 x 15 cm) was connected to the main water supply that circulated throughout the laboratory. A 5-cm circular target of translucent Plexiglas was located at one end of the tank. The target was mounted on a stainless steel rod screwed into the needle holder of a crystal phonograph cartridge. The output was connected to a response detector circuit provided by Life Science Associates after the model developed by Woodard and Bitterman (1974). Each target strike sent a signal to an input-output device that was constructed for the Apple port. It consisted of a versatile interface adapter (VIA r6522) that could sense a low-high state on eight input lines and eight transistor-transistor logic outputs connected to appropriate solid-state switches. The interface was connected to an Apple IIe microcomputer.

Reinforcement consisted of a 5-mm length of pelleted catfish food blended with equal amounts of water. The reward was pumped (Cole-Parmer Masterflex peristaltic pump, Model 7543-30) from a 0.5 L container through a length of Tygon tubing (Cole-Parmer No. 6419-16) to the center of the target. The bottom of the target was located 5 cm from the bottom of the tank. The target was illuminated from behind by a bulb in a funnel. The inside of the funnel was lined with aluminum tape so that the light showed out the narrow end. The stimuli included diffuse blue, green, or red light produced a 25-W, 120 V bulb

manufactured by General Electric.

A photocell and light source were placed 75 cm from the target end of the tank and 32 cm from the opposite end, 10 cm from the bottom of the tank. A plastic barrier was placed directly below the level of the photocell and light beam at a height of 6 cm. This barrier insured that the fish, if it swam to the back of the tank, would pass through the light beam. When the fish broke the light beam, output from the photocell was sent to a swim-by detector circuit manufactured by Life Science Associates. Output from the swim-by detector was sent to the input-output interface of the microcomputer. A top, constructed of pegboard, was fastened to the tank to reduce ambient light and improve the salience of the light stimuli and the sensitivity of the photocell.

Procedure

To condition the target strike response, goldfish were placed in the operant tank for 1 hr per day during which they received free food every 2 min and reinforcement for each target strike. Following this two-week training phase, all subjects received discrimination training in which a multiple variable time (VT) 30 s EXT schedule was programmed. In this schedule, during the VT component, the fish received response independent reward every 30 sec on average in the presence of an exteroceptive stimulus, either a red or a green light. During the extinction segment, fish received no food in the presence of a different exteroceptive stimulus, either green or red. In each 40 min session, subjects received five 4-min segments of the VT schedule and five 4-min segments of EXT. The VT and EXT segments were presented randomly according to Gellerman orders. All subjects received 40 sessions of the discrimination phase.

While responding was not required to receive reinforcement, all subjects came to strike the target during discrimination training. Consequently, following the discrimination phase, subjects were matched according to response rates and assigned randomly to one of two groups. Subjects in group OBSERVE were trained on a mixed VT 30 s EXT schedule. In this schedule, fish received 10 randomly alternating 4-min segments of either VT 30 s or EXT in the presence of a blue light. For one half of the subjects, if the fish broke the light beam at the other end of the tank, the light changed from blue to red for 30 s if the food component was in effect. For the other one half, the light changed from blue to green. If the extinction component was in effect, the light changed from blue to green for one half of the fish or from blue to red. Each photocell crossing extended the presentation of S+ or S- for 30 s regardless of which stimulus was present at the time of crossing. If

a segment change occurred during the 30 s period that S+ or S- was being presented, the stimulus changed to the appropriate stimulus. That is, if the fish had produced red to indicate that the food component was in effect, the target color changed to green if the next segment called for extinction, or continued red, if the food component remained.

Subjects in group NOT OBSERVE were trained on a multiple VT 30 s EXT schedule. These subjects received 10 randomly alternating 4-min segments of either the food component or the extinction component each in the presence of a different exteroceptive stimulus. If the fish broke the light beam, the red or green light changed to blue for 30 s. Each additional photocell crossing extended the presentation of the mixed stimulus for 30 s. If a segment change occurred during the 30 s period that the mixed stimulus was being presented, the mixed stimulus remained engaged. Subjects experienced 40 sessions under these conditions.

Following this procedure the experimental conditions were reversed. Fish in group OBSERVE could terminate for 30 s the presentation of S+ and S- by crossing the light beam, while fish in group NOT OBSERVE could produce for 30 s, S+ and S-. Again forty sessions were carried out. During the course of the experiment, two goldfish died. One died during the discrimination phase and one during the reversal phase.

RESULTS

Photocell crossings were recorded during the discrimination phase to determine a baseline rate of photocell crossings during a condition where crossings had no effect on stimuli or reward availability. Results from a split-plot analysis of variance revealed no statistically reliable difference in crossover rates between VI and EXT segments, $F(1,9) = 3.06$, $p > .05$. The average crossover rate during VI segments was 28.53, while the average crossover rate during extinction was 42.08. The lack of significance can be attributed to high variability; the fish sometimes showed high crossover rates followed by very low rates.

Crossover rates during the observing response procedure proper were analyzed by using a split-plot analysis of variance (ANOVA) with two within factors and one between factor. The within factors included Segment Type (VT or EXT) and Blocks (blocks of five days over the final twenty sessions). The between factor was Groups (OBSERVE or NOT OBSERVE). A probability level of $p < .05$ determined significance. Figure 1 depicts the observing response rates per session for groups OBSERVE and NOT OBSERVE during the food components and the extinction components. The Groups by Segment Type

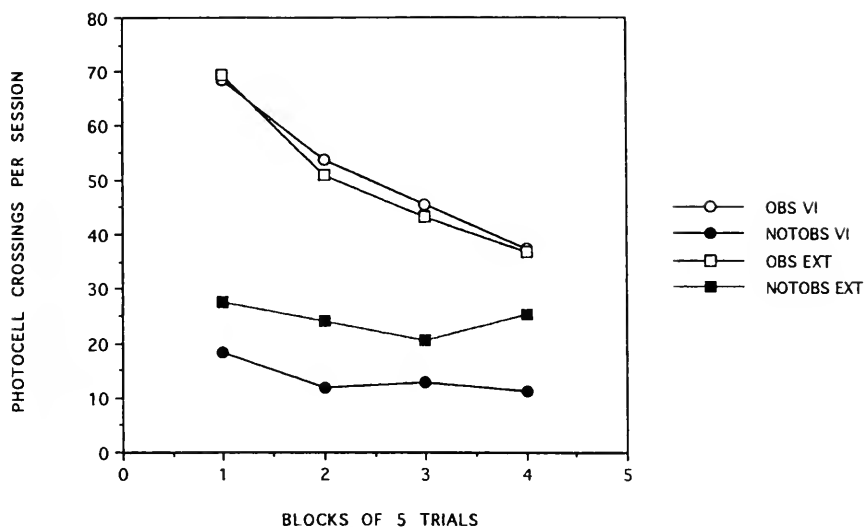


Figure 1. Mean observing responses per session for groups Produce and Terminate during variable time (VT) and extinction (EXT) segments. Data are from the acquisition phase of Experiment 1.

interaction was significant, $F(1,9) = 6.73$, $p < .05$ and is accounted for by two major trends. First, there was no difference in observing rates during the food and extinction components for group OBSERVE subjects. The mean observing rate for VT segments was 51.29 whereas the mean observing rate during EXT segments was 50.08. Second, there was a significant difference between VT and EXT segments for Group NOT OBSERVE. Fish terminated presentations of S- at a significantly higher rate than they terminated presentations of S+. Average photocrossing rate per session during food segments was 13.54, whereas the average rate during extinction segments was 24.26.

During the reversal phase, fish in Group OBSERVE terminated S- at a higher rate than they terminated S+. This was also true for NOT OBSERVE subjects though there was a trend for the observing rates to converge. The mean observing rates for each segment for each group were 22.40 (OBSERVE S+), 31.49 (OBSERVE S-), 20.92 (NOT OBSERVE S+), and 27.04 (NOT OBSERVE S-). The ANOVA revealed only a significant Segment Type effect, $F(1,8) = 15.09$, $p < .05$. Observing rates during extinction segments were higher than were observing rates during the food segments. The average observing rate during extinction was 29.27 and the average rate during the VT segment was 21.66.

DISCUSSION

Goldfish produced presentations of S+ and S- at the same rate, with a tendency for the observing rates to decline across sessions. Since the schedule of reinforcement for these subjects was a mixed schedule, fish could not differentially produce S+ or S-. If S- is aversive, as suggested by the conditioned reinforcement hypothesis, then one might expect observing rates to decline when one half of the responses resulted in punishment.

Fish terminated S- significantly more often than S+. This result is consistent with the conditioned reinforcement hypothesis that S- may be aversive and supports the finding by Purdy and Peel (1988, Exp. 1) that for fish baseline rates of responding to a target that produced no food were decreased by presentations of S-. Data from the reversal phase were consistent with the acquisition data. Group OBSERVE terminated S- significantly more than S+. Group NOT OBSERVE tended to produce S- at a higher rate than they produced S+ though the difference was not significant.

While the data from Experiment 1 supported the contention that fish find S- aversive, they may not have crossed the light beam to terminate S- more than S+. Rather, they may have crossed the photocell less during S+ because to terminate a positive stimulus was aversive. A third explanation offers that fish may have crossed the photocell more during extinction because there was nothing else to do. Since food would not be available for four minutes, the fish may simply have swum around until the food segment was presented. In Experiment 2, we controlled for these possibilities using a yoked control procedure. In this procedure, the master fish can terminate presentations of S+ or S- by passing through the light beam. The yoked fish, on the other hand has S+ and S- terminated at the same time as the master fish, but its photocell crossings are not correlated with stimulus termination. If the yoked fish cross the photocell during the food segment more than the master fish, then we have evidence that crossing the photocell during S+ is aversive. If master fish cross the photocell more during extinction than the yoked fish, then we have evidence that S- is aversive.

In addition, we tested whether fish would terminate S- when reward was response dependent. If the master fish terminate S- at a high rate and consequently respond more during extinction segments, this would suggest that fish find S- aversive. The finding would suggest further that even though fish could improve their response efficiency by not responding during extinction segments, they would not.

EXPERIMENT 2

METHODS

Subjects

Sixteen goldfish (*Carassius auratus*) 10 to 15 cm in total length were obtained from the B and P Minnow Farm and were housed as in Experiment 1.

Apparatus

The apparatus consisted of two identical operant conditioning tanks measuring 24 x 46 x 22 cm, inside dimensions. The tanks were constructed of wood, lined with plastic and sealed with silicon sealant. They were connected to the main water supply that circulated throughout the entire laboratory. In each tank, a 5 cm circular target of translucent Plexiglas was located in the middle of one end. The bottom of the target was 3 cm from the bottom of the tank. A photocell and light source was located 34 cm from the target end of the tank and 8 cm from the bottom of the tank. A barrier was positioned 3 cm below the photocell to ensure the fish had to pass through the light beam. All other details were the same as those in Experiment 1.

Procedure

Goldfish were randomly assigned to either the master group or the yoked group and were trained to target strike as previously described. In Phase 1, all subjects received 40-min sessions in which a multiple variable interval (VI) 10 s EXT schedule was programmed on the target. In this schedule, during the food component, the fish received a reward for the first response following an average interval of 10 s in the presence of a red light. A greater density of reinforcement was used in this experiment to ensure a good discrimination between food and no food segments. During the extinction segment, the fish received no food in the presence of a green light. All subjects received five 4-min segments of the VI schedule and five 4-min segments of EXT. Segment type alternated randomly according to Gellerman orders. All subjects received 70 sessions of discrimination training.

In Phase 2, subjects in both groups Master and Yoked continued to be reinforced through independently programmed multiple VI 10 s EXT schedules. When the Master fish crossed the light beam during the food component, S+ was terminated for 30 s in both the master tank and the

yoked tank. When the Master fish passed in front of the photocell during the extinction component, S- was terminated for 30 s in both tanks. All subjects experienced 50 sessions under these conditions. Following this phase, the experimental conditions were reversed. Fish that had been the master fish became yoked controls and fish that had been yoked controls served as master fish. Twelve sessions of Phase 3 were conducted.

During the course of the experiment it became necessary to eliminate three pairs of fish. Two of the fish died during the course of the experiment and two fish stopped responding for food. Five pairs of fish completed the experiment. It was not necessary to change a fish's group from Master to Yoked or vice versa.

RESULTS

The number of photocell crossings per session and discrimination ratios were analyzed by using split-plot ANOVAs with one between factor and two within factors. The between factor was Group (Master vs. Yoked) and the within factors included Segment Type (VI or EXT) and Blocks (blocks of two trials). A probability level of $p < .05$ was considered significant.

During Phase 2, master fish and yoked controls crossed the barrier at virtually the same rate during extinction segments, but during VI segments, master fish crossed the barrier significantly less often than yoked fish. Master and yoked subjects crossed the barrier 14.43 and 14.93 times per session during extinction, respectively. During VI segments master and yoked subjects crossed the barrier 11.22 and 15.84 times, respectively. The data resulted in a significant Group by Segment Type interaction ($F(1,8) = 23.52$). Figures 2 and 3 show that there was a large difference in the degree of error variability between master and yoked fish. The standard deviations for the master fish for the VI (6.26) and EXT (6.76) segments were much smaller than the standard deviations for the VI (16.15) and EXT (15.57) segments for the yoked controls. Overall, fish crossed the barrier more during extinction (14.68 per session) than during VI segments (13.52), $F(1,8) = 7.46$.

The results of reversing the experimental conditions for the master and yoked fish were consistent with the findings of Phase 2. The new master fish began terminating S- (14.82 per session) at a higher rate than S+ (12.53 per session). Additionally, the new yoked controls crossed the photocells indiscriminately during VI (15.62 per session) and EXT segments (16.37 per session). Again the standard deviations revealed that the master fish had lower response variability than yoked fish. The

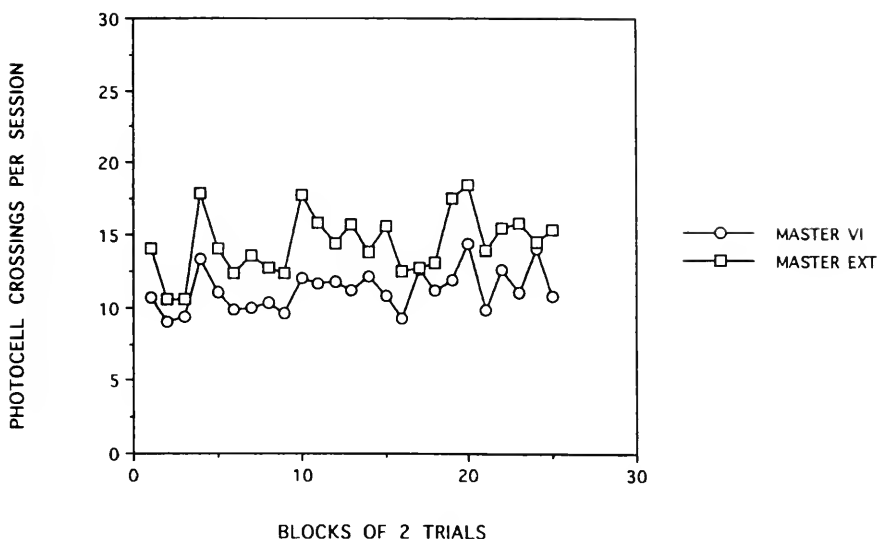


Figure 2. Mean photocell crossings for master fish during Variable Interval (VI) and EXT segments. Data are from Phase 2 of Experiment 2.

standard deviations for master fish were 7.18 and 8.11 for VI and EXT segments, respectively. For the yoked fish the standard deviations were 21.31 and 20.57 for VI and EXT segments, respectively. Because of the high degree of variability an overall split-plot analysis of variance revealed no differences attributable to any variable. However, if only the master fish scores were analyzed, there was a significant difference in Segment Type, $F(1,4) = 10.75$). The analysis showed that master fish terminated S- significantly more than S+. The analysis for the yoked controls was not significant, $F(1,4) < 1$.

Discrimination ratios were determined by dividing the total number of responses produced during the VI segments by the total number of responses produced during both VI and EXT segments. These ratios were subjected to a split-plot analysis of variance. The discrimination ratios did not differ significantly between the master and yoked fish over the final 20 sessions of Phase 1. The mean discrimination ratio for the master fish was .67, while the mean ratio for the yoked controls was .71. The discrimination ratios during Phase 2 also did not differ significantly. The mean discrimination ratio for the master fish was .73, and for the yoked fish the mean ratio was .78. Finally, the discrimination ratios during the reversal phase also did not differ statistically. The trends were reversed, however, as the mean discrimination ratio for the new yoked fish was .78 and the mean ratio for the new master fish was .73.

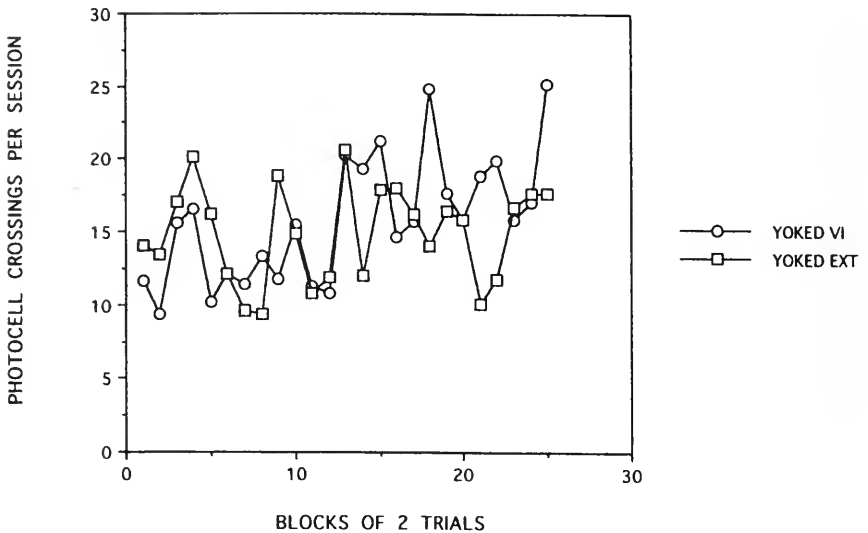


Figure 3. Mean photocell crossings for yoked fish during VI and EXT segments. Data are from Phase 2 of Experiment 2.

DISCUSSION

Master fish crossed the barrier during VI segments less often than yoked fish, which suggested that termination of S+ may have been aversive. Indeed, yoked fish crossed the photocell during VI segments at a slightly higher rate than they did during extinction. This finding suggests that fish do not differentially terminate a stimulus simply because there is nothing else to do. Whereas master and yoked fish crossed the barrier during EXT segments at virtually the same mean rate, the variability for the master fish was substantially less. Taken together, the findings suggest that crossover behavior by the master fish was controlled by changes in stimulus contingencies, whereas crossover behavior in the yoked fish was not.

Consistent with Experiment 1, there was no evidence that S- was rewarding. Master fish terminated S- even though it reduced somewhat their ability to discriminate between segments of food and extinction. Thus, even under conditions where reward is response dependent and termination of S- could decrease response efficiency, fish terminated S-. These results support our contention that cognitively less complex animals may not find S- rewarding even though its presentation could lead to improved response efficiency.

GENERAL DISCUSSION

The present findings are compatible with the conditioned reinforcement hypothesis. This theory correctly predicts that S- should not support observing and that it may be aversive. Additionally, the findings suggest that fish do not find a stimulus rewarding if the stimulus is associated with extinction and an opportunity to improve response efficiency. In this regard, the goldfish data are consistent with pigeon data showing that S- will not support observing even if it can lead to increased response efficiency (Browne & Dinsmoor, 1974; Dinsmoor, Browne & Lawrence, 1972; Mulvaney, Dinsmoor, Jwaideh & Hughes, 1974).

It remains to be determined why primates find an increase in response efficiency rewarding while fishes and pigeons do not. At least two explanations exist. First, fishes and pigeons may find increases in response efficiency to be rewarding, it is just that the level of effort required to produce reward is too low to make a difference. If observing is to have a beneficial effect on behavior by reducing energy expenditure, then the effort required to make the observing response must be less than the effort to respond under conditions of no reward. At the very least there must be a savings of energy to maintain the observing response. This may not be the case in the pigeon studies, as evidenced by the findings of Dinsmoor, et. al., (1988). Dinsmoor's pigeons responded on the observing key to produce stimuli correlated with a VT 60 sec schedule and extinction. Pigeons could also observe when the two schedules were VI 60 sec and extinction. In a third condition, pigeons could observe when the schedules were VI 60 sec and VT 60 sec. Observing was maintained at a high rate when a food schedule (VI 60 sec or VT 60 sec) was paired with an extinction schedule, but not when two food schedules were paired. The results from the VT/VI condition showed that pigeons will not observe when the sole outcome was an opportunity to improve response efficiency. Dinsmoor, et. al. (1988), pointed out that, in most instances, a pigeon's response rate increases during the positive component of a multiple schedule and decreases during the extinction component. Because of these changes, the overall rate of pecking in a multiple schedule is greater than the overall rate of pecking in a mixed schedule (Bower, McLean, and Meacham, 1966; Dinsmoor, Browne, and Lawrence, 1972; and Hirota, 1974). This finding would indicate that the pigeon might not save energy by observing.

The second explanation is that there may exist differences with respect to the variables that maintain observing in fishes, pigeons and primates. The explanations proposed to account for the maintenance of

the observing response that have received the most support in the literature include the conditioned reinforcement hypothesis (Fantino, 1977; Wyckoff, 1952) and the uncertainty reduction hypothesis (Berlyne, 1957; Hendry, 1969; Schrier, Thompson, & Spector, 1980). Dinsmoor (1983) and Fantino (1977) have documented convincingly that the most viable explanation for the maintenance of the observing response is the conditioned reinforcement hypothesis. Left unanswered, however, is what constitutes conditioned reinforcement. The argument presented here suggests that for fishes and pigeons a stimulus associated with food can serve as a conditioned reinforcer, but a stimulus associated with a reduction in energy expenditure will not. For primates on the other hand, a stimulus associated with either a food reward or a reduction in energy expenditure will serve as a conditioned reinforcer. Thus, while conditioned reinforcement theory offers the best account for the maintenance of observing, there may exist differences between species in what constitutes the nature of the primary reward supporting the conditioned reinforcer.

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AFFILIATION AS AN INTERVENING VARIABLE: COVARIATION IN MEASURES OF AFFILIATION IN A REPRODUCTIVE AND A NONREPRODUCTIVE GROUP OF RHESUS MACAQUES (*Macaca mulatta*)

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ABSTRACT: Affiliation is often used as an intervening variable in behavioral studies of nonhuman primates. Variables used to measure affiliation should be strongly correlated if it is a valid intervening variable. Social context also should not strongly influence relationships between variables used to measure affiliation. Few studies have, however, reported either the correlations between variables used to assess affiliation or the influence of social context on relationships between the variables. Correlations between affiliative variables were therefore calculated on data from two groups of rhesus (*Macaca mulatta*) and influences of social context on these correlations were assessed.

Affiliation was measured with 7 variables. Two methods were used to investigate the influence of social context: Analyses were made of interactions between several age/sex categories of individuals. Comparisons were made between an experimental group and a matched control group. There were higher rates of sexual behavior in the experimental group. The mature males in the experimental group were vasectomized so females did not conceive. In this group females had repeated nonpregnant estrous cycles. Males were intact in the control group. In this group the mature females conceived and were pregnant during data collection.

The variables were significantly correlated across all social contexts. Affiliation may therefore be a useful intervening variable. The magnitude of the correlations between variables did vary considerably across social contexts. Sometimes the sign of the correlations between measures changed as a function of social context. Analyses of individual variables and their interrelationships may therefore be necessary for detailed understanding of the meaning of affiliative interactions in nonhuman primates.

Primatologists often define affiliation by elaboration of the measures used for its assessment (O'Keeffe, Lifshitz, & Linn, 1983;

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Baker & Estep, 1985; Ehardt & Bernstein, 1987; Crooks & Rasmussen, 1991). Proximity and grooming are probably the most universally used measures of affiliation (Carpenter, 1942a; Rasmussen, 1984; Hill, 1986; Byrne, Whiten, & Henzi, 1989). Measures of behavioral patterns associated with proximity (such as approaches, leaves and follows) and grooming presents, presents, and mounts are sometimes used to assess affiliation (Rasmussen, 1984; Chadwick-Jones, 1989). Vocalizations have also been used to assess affiliation (Biben, Symmes, & Masataka, 1986; Masataka & Biben, 1987). These affiliative variables share three characteristics: They are associated with either distance reduction or proximity maintenance, they do not evoke escape responses, and they are not agonistic behavioral patterns.

Affiliation is an intervening variable (MacCorquodale & Meehl, 1948; Miller, 1959; Hinde, 1985) since it is a tendency that is assumed to be assessed by variables having these three characteristics. An intervening variable is a convenient label used to describe several variables that are closely related to each other (Deese & Hulse, 1967).

Affiliation might be defined as a social centripetal tendency responsible for individuals forming into groups and staying in groups that is not agonistic. This definition does not make a necessary link between affiliation and an influence on an individual's Darwinian or inclusive fitness (Hamilton, 1964; Tinbergen, 1965; Rasmussen, 1988). This definition does not exclude sexual interactions.

If affiliation is a useful intervening variable, it must provide a fuller understanding than if the variables used for its measure are not assumed to assess aspects of the same tendency. The process of assessment of the validity and usefulness of an intervening variable involves many steps (Suen & Ary, 1989).

Dominance is an intervening variable that has both gone through some of these steps and that has been often used in studies of nonhuman primates (Altmann, 1962; Bernstein, 1981; Boyd & Silk, 1983; Cowlshaw & Dunbar, 1991). Much less attention has been directed to evaluation of affiliation as an intervening variable. There are many reasons why greater attention should be devoted to this task. The results of the analyses in this article bear on four of these reasons.

First, an intervening variable is a label used to describe a number of variables that are closely interrelated. Only incomplete information is available on the relationships between measures used to assess affiliation. Many who use measures of affiliation have spent years watching their subjects and hence have an excellent sense of the appropriate measures to use to assess affiliation. Yet a quantitative knowledge of the interrelationships between variables would provide useful additional support for choice of appropriate measures.

Second, the distinction between affiliative and sexual behavior is ambiguous in the literature. Sexual behavior is functionally defined as behavior that has been associated with conception during the phylogenetic past (Scott, 1956; Tinbergen, 1965; Rasmussen, 1984). Presents and mounts are patterns of behavior that are sometimes sexual that have received considerable attention as measures of affiliation. Perhaps this is so because they do not neatly fit into any single behavioral category (Marler, 1968). This is particularly true for intrasexual presents and mounts (Reinhardt, Reinhardt, Bercovitch, & Goy, 1986; Chadwick-Jones, 1989) since they are not sexual within a functional definition of sexual behavior (Rasmussen, 1984).

Third, knowledge of the social context of an affiliative interaction may be essential for understanding its meaning. Sex of interactants may, for example, influence the meaning of an affiliative interaction. Male => male or female => female mounts could, for example, have a different association with other measures of affiliation than do male => female mounts or female => male mounts. [=> symbolizes directional behavioral interactions. Male grooms of females are therefore symbolized as male => female grooming. <=> symbolizes bidirectional behavior or a measure of the distance between a dyad. When, for example, analyses are focused on grooming of males by females and grooming of females by males this is symbolized as male <=> female grooming.] It also may be necessary to know the reproductive status of the interactants and the reproductive state of the group in which they interact to evaluate affiliative interactions. Adult male grooming of adult females in estrus could, for example, have a different meaning than adult male grooming of pregnant females (Smuts, 1985). If social context does have a strong influence on the relationship between measures of affiliation then assessment of the measures, and the context in which they occur, may be necessary for accurate assessment of affiliation.

Fourth, if an intervening variable is found useful, it may help us to understand underlying design features (Tooby & Cosmides, 1990) of primate social organization. Intervening variables help group variables that together characterize possible adaptive aspects of primate social organization, such as their coherence (Zuckerman, 1932).

Analysis of the correlations between several measures of an intervening variable is an essential step toward evaluation of its utility (Hinde and Datta, 1981). If several measures are strongly related, then there is greater confidence in the intervening variable as an explanatory tool.

All the analyses presented here are centered on the correlations between 7 measures of affiliation. Five of these are frequently used to

measure affiliation: Two are measures of mean distance between pairs, the third is the combined rate of approaching, leaving and following, the fourth is grooming and the fifth grooming presents. The other two are presents and mounts. Presents and mounts are sometimes used as measures of affiliation, sometimes as measures of sexual behavior and sometimes as measures of agonistic behavior.

The analyses focus on the degree to which one measure of affiliation between pairs predicts their affiliation by the other measures: If, for example, monkey "A" grooms monkey "B" more than monkey "C", does monkey "A" also more frequently solicit grooming with grooming presents to monkey "B" than to "C"? That is, if there is a transitive (Boyd & Silk, 1983) grooming relationship between "A", "B" and "C", does this transitive relationship also hold for solicitations of grooming?

The measures of affiliation are initially assumed to be reciprocal (Hinde, 1987). This is only an initial assumption. More complex relationships are both possible and probable (Seyfarth, 1977). If, for example, monkey "A" both presents to and mounts monkey "B", then the presents and mounts are reciprocal. If monkey "A" presents to monkey "B" and is mounted by monkey "B", but neither receives presents from monkey "B" nor mounts monkey "B" then the presents and mounts are complementary (Hinde, 1987).

Focus on the correlations between variables provide information on the first two reasons why affiliation should be more closely examined as an intervening variable. First, examination of the magnitude of the correlations assesses the degree to which several measures of affiliation are related and hence the extent to which they may all measure a shared affiliative tendency. Second, examination of the strength of correlations between presents and mounts and the other measures helps show the degree to which these variables assess similar affiliative tendencies.

Analyses of the data as a function of interactants' age and sex is one method used to investigate influences of social context, the third reason affiliation should be more closely examined as an intervening variable. Comparisons are also made between a sexually active group and a matched reproductive group. Females in the sexually active group did not conceive because the reproductively mature males were vasectomized. Mature females in this group had repeated nonpregnant estrous cycles and engaged in sexual behavior during each cycle (Michael & Zumpe, 1988). Sexually mature females in the reproductive group conceived and were pregnant throughout the duration of observations. There were therefore significantly higher rates of sexual behavior in the group containing the vasectomized males (Rasmussen & Goy, 1988; Rasmussen, 1993 a,b).

METHODS

Animals and Housing

The sexually active group was composed of a 5 year old vasectomized male, a 4 year old vasectomized male, an intact 2 year old male, four 4 year old females, one 3 year old female, and three 2 year old females. The matched reproductive group had the same age and sex composition but all males were intact. Thus the experimentally manipulated difference between groups was male fertility.

There were 24 menstrual cycles among the mature females in the sexually active group. Forty-six consorts and 14 ejaculations occurred in the group during data collection. In the reproductive group, there were 4 menstrual cycles among the mature females. There were 27 consorts and 3 ejaculations in the group during data collection.

Subjects were selected so they could be closely matched with a paired individual. Matching was by sex, age, weight and housing history. All females were nulliparous and thus did not vary in parturitional, lactational, or infant rearing experience. One member of each matched pair was placed in the sexually active group and the other in the reproductive group.

The groups were housed in identical indoor pens. These were 6.7 m in length, 2.5 m in width and 2.6 m in height. The pens were separated by a minimum distance of 1.2 m and in a room with two additional identical pens containing breeding rhesus groups. Lights were automatically turned on at 6 am and turned off at 6 pm. Two frosted windows next to the pens let in ambient light.

The 5 and 4 year old males in both groups copulated to ejaculation. The 4 and 3 year old females in the reproductive group conceived. Although young, all group members, except 2 year olds, were sexually mature to the extent that they were potentially capable of reproduction.

Behavioral Sampling

All subjects were observed from outside the pens for more than a year before this experiment. I habituated them to my presence for 3 weeks before data collection. The data were collected from January 2, 1987 until the day before the birth of the first infant in the reproductive group, June 1, 1987. Data were collected on a lap top computer for 5 days each week from 15.00 to 18.00 hours. I collected all data except those on the menstrual cycles of the females. The latter are routinely collected on all rhesus at the primate center.

Individual group members were the focus of 14 min sampling

sessions. The sessions were divided into seven 2 min sampling intervals. A mean of 7.28 (SD=2.28) sampling sessions were conducted each day of data collection. The focal subjects of the sampling sessions were selected sequentially from a list of all individuals in both groups. Focal sampling (Martin & Bateson, 1993) was used for the variables requiring constant subject monitoring. Concurrent samples (Hausfater, 1974; Chapais, 1986) were collected on all occurrences of variables (Martin & Bateson, 1993) that could be simultaneously monitored for all group members. An auditory cue was programmed into the lap top 15 seconds before the beginning of the next 2 min interval to sharpen focus on variables sampled instantaneously at the onset of the next interval. The analyses are based on 2445 2 min interval samples collected during the 14 min sampling sessions.

The definitions of the affiliative variables used during data collection are provided in the appendix. The unit of observation and the method used to sample the variables are summarized in Table 1. All analyses are based on summary descriptive statistics. The present rate of "A" to "B" was, for example, calculated by dividing all observations of presents of "A" to "B" from focal sampling sessions on "A" and "B" by the sum of 2 min intervals collected during those sampling sessions.

Table 1. Variables, Observation Method and Sampling System

Variable	Unit of Observation	Sampling Method
1. Nearest Neighbor Distance	individual-focal	instantaneous
2. Close Distance to Nearest Neighbor	individual-focal	instantaneous
3. Approaches, Leaves & Follows (ALF)	individual-focal	frequency
4. Grooming	all individuals	I/O (concurrent)
5. Grooming Presents	individual-focal	frequency
6. Presents	individual-focal	frequency
7. Mounts	all individuals	frequency (concurrent)

Statistical Control of Previous familiarity before Group Formation

In an ideal study there would be no differences between the sexually active group and the reproductive groups except those associated with

the experimental manipulation: vasectomization of the mature males in the sexually active group. Groups of nonhuman primates cannot yet, however, be as closely matched as, say, groups of inbred rodents. Previous studies in which matched groups are compared have seldom used subjects as closely matched as those in this project, matching made possible by the large population of rhesus maintained by the primate center.

A systematic difference was found between the two groups during data analyses: some pairs of individuals were housed with each other for more days before group formation. This nuisance variable is referred to as previous familiarity. The influence of previous familiarity was statistically controlled (Cohen & Cohen, 1983) by using the residuals from the regression of the affiliative interactions on this nuisance variable. Transformations were used, when appropriate, to normalize the residuals. Linear and quadratic fits were tried for every dependent variable. For all dependent variables, except grooming, the quadratic aspect of previous familiarity did not appreciably increase R^2 ; therefore only linear fits were used. Grooming rate was regressed on both the linear and quadratic aspects of previous familiarity. All descriptive and inferential statistics use the residualized variables. Tests of significance and interpretation of the influence of previous familiarity on affiliation have been published elsewhere (Rasmussen, 1993a).

Analytic Strategy

Several methods are used to describe and analyze relationships between measures of affiliation and differences in these relationships between groups. These methods were first applied to all members of each group and then to dyads composed of various age/sex classes, such as female => male interactions. As in Fisher's protected t-test, tests of significance were not conducted on subcategories of dyads unless the tests conducted on all dyads, and on the immediately higher dyad types, were significant (Cohen & Cohen, 1983; Rasmussen, 1984). Each set of analyses is followed by a brief discussion. A general discussion compares results across all dyad types.

Spearman Correlations between Variables: One analytic focus is the degree ordinal patterns of affiliation between monkeys are correlated with those evaluated by other measures of affiliation. If monkey "A" grooms "B" more than "C", is "A" also likely to more frequently grooming present to "B" than to "C"? Spearman correlation coefficients (Siegel & Castellan, 1988) are used to describe these relationships between all possible pairs of the 7 affiliative variables for directional dyads in each group. Interactions directed by one individual to another

are called directional dyads (Koyama, 1991). Affiliative interactions directed by the oldest male to the oldest female are therefore a directional dyad. There were 21 correlations possible between the 7 measures of affiliation.

The distance from "A" to "B" is the same as the distance of "B" to "A". There were therefore 55 ($[11 \times 10]/2$) nondirectional dyads on which nearest and close neighbor distances could be calculated in each group. Duplicate values of neighbor distances were matched with directional behavioral interactions so relationships between distances and affiliative interactions could be described.

Trends in association between Measures of Affiliation within Groups: Overall trends in the association between measures of affiliation within groups were also evaluated. Was, for example, there a trend for stronger correlations between measures of male \Rightarrow male affiliation in the reproductive group than in the sexually active group? Three methods are used to evaluate such trends.

First the signs of the 21 correlations between the measures of affiliation within groups are used as a simple description of the direction of relationships. Distances to neighbors decrease with greater affiliation, and all the behavioral measures increase with greater affiliation. If the measures assess the intervening variable affiliation, then measures of distance to neighbors should be positively correlated; behavioral measures of affiliation should be positively correlated, and the measures of distance to neighbor and the behavioral measures should be negatively correlated.

Second, similarity in the way dyads were ranked by the affiliative variables is assessed with the Kendall Coefficient of Concordance, W (Siegel & Castellan, 1988). W provides a measure of the consistency with which the variables rank dyadic interactions. W was calculated by ranking dyads by Nearest Neighbor Distance and Close Nearest Neighbor Distance in descending order and the other variables in ascending order.

Third, the mean strength of agreement between each measure of affiliation and the 6 others was determined. The mean of the means of the squared correlations with the other variables was used for this task. The squared Spearman correlations indicate the proportion of variation shared in ranks of directional dyads as they are ordered by two variables. Correlations between variables opposite to those expected were given a value of 0 before calculating the mean. The mean squared correlation may be interpreted as the mean proportion of affiliative variation shared between dyads ranked by one variable and all others. This measure provides an empirical guide to determining which measure of affiliation tended to be most strongly associated with the others.

The three methods overlap. Each evaluates trends in the association between measures of affiliation. However, by looking at the patterns from different, but overlapping, perspectives it was possible to have a more complete knowledge of the complex patterns of rhesus affiliation.

Comparison of Patterns of Affiliation between Groups: Another focus of the analyses is similarity in relationships between measures of affiliation in the sexually active group and the reproductive group. Did, for example, the mature females in both groups tend to present at a higher rate to the females who they also mounted at higher rates?

A Pearson correlation was calculated between the Spearman correlation matrices from the groups in order to assess the overall similarity in the relationships between the variables. This correlation between paired values of correlation coefficients is called the matrix correlation. Like all correlations (Cohen & Cohen, 1983), matrix correlations are not influenced by linear transformations of the coefficients in either matrix. Similarities in relative values of correlation coefficients are therefore assessed. The significance of the matrix correlations was determined on the basis 10,000 random permutations of the matrices (Dow, Cheverud, & Friedlaender, 1987; de Waal, 1991).

Differences between groups in the mean squared correlations for each measure of affiliation are also calculated. These show the degree relationships between the measures were influenced by differences between groups. The greatest difference in correlations between groups is used to show the relationship between variables most influenced by the difference in social contexts between groups.

RESULTS

All Dyads

The first set of analyses was conducted on all 110 directional dyads in each group. The matrix correlation was $+0.95$ ($p < .001$). In both groups all 21 correlations between the variables were in the expected reciprocal direction (Table 2). The coefficient of concordance was slightly less in the sexually active group ($W = +0.50$, $p < .001$) than in the reproductive group ($W = 0.55$, $p < .001$).

All affiliative measures in the reproductive group, except close neighbor distance, had stronger mean squared correlations. The correlation between grooming present and present rates differed most between groups. There was a moderate reciprocal relationship ($+0.47$) between these variables in the reproductive group. There was only a weak tendency in this direction in the sexually active group ($+0.10$).

Table 2. Affiliation between All <=> Dyads.

Spearman Rank Order Correlation Coefficients between the Variables and the Mean Squared Correlations of the Variables. Upper Half Matrix, Reproductive Group; Lower Half Matrix, Sexually Active Group; Sr^2 and Rr^2 are the mean of the squared correlation coefficients between the row variable and the other 6 variables for the Sexually active (S) and Reproductive (R) groups; $Diff = Sr^2 - Rr^2$.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+ .69	-.88	-.79	-.45	-.38	-.21	+.35	+.38	-.03
2. Close Neighbor	+ .79		-.58	-.59	-.45	-.25	-.14	+.27	+.24	+.03
3. ALF Rate	-.80	-.66		+.75	+.48	+.49	+.35	+.33	+.38	-.05
4. Grooming Rate	-.70	-.60	+.65		+.29	+.47	+.19	+.25	+.31	-.06
5. Grooming Present Rate	-.27	-.13	+.37	+.16		+.47	+.38	+.09	+.18	-.09
6. Present Rate	-.46	-.36	+.44	+.46	+.10		+.55	+.13	+.20	-.07
7. Mount Rate	-.28	-.17	+.41	+.04	+.50	+.19		+.09	+.11	-.02

The relative values of correlation coefficients in the matrices from the two groups were remarkably similar. Monkeys who tended approach, follow or leave each other, for example, also tended to be closer to each other in both groups.

The rank orders of directional dyads by each of the 7 measures of affiliation were significantly concordant in both groups. Variables in the reproductive group were slightly more concordant, and the mean squared correlations were larger in the reproductive group for 6 of the 7 variables.

Sexually Mature Dyads

The sexually mature group members seemed likely to be those whose affiliative interactions might differ most between groups since these were those whose reproduction differed. Analyses were therefore conducted on the 42 directional dyads in each group that did not contain 2 year olds.

The correlation between the two matrices was +.92 ($p < .001$). In the sexually active group, 19 of 21 correlations between variables were in the expected reciprocal direction; all correlations were in the expected direction in the reproductive group (Table 3). The concordance in the reproductive group was identical with that calculated on all dyads

Table 3. Affiliation between All <=> Dyads not containing 2 Year Olds.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		+.78	-.89	-.79	-.35	-.60	-.31	+.32	+.43	-.11
2. Close Neighbor	+.63		-.62	-.71	-.47	-.29	-.14	+.18	+.30	-.13
3. ALF Rate	-.82	-.54		+.81	+.36	+.59	+.24	+.29	+.39	-.10
4. Grooming Rate	-.71	-.53	+.64		+.32	+.58	+.20	+.28	+.38	-.10
5. Grooming Present Rate	-.37	-.12	+.38	+.28		+.32	+.14	+.10	+.12	-.01
6. Present Rate	-.42	-.26	+.32	+.62	-.13		+.33	+.12	+.22	-.10
7. Mount Rate	-.21	-.03	+.34	+.04	+.48	-.18		+.06	+.06	+.01

($W=.55, p<.001$); the concordance of the variables in the sexually active group was smaller ($W = .45, p<.001$). There were larger mean squared correlations between all variables in the reproductive group except mount rate. The correlation between present and mount rates differed most between groups. Presenting and mounting were faintly complementary in the sexually active group ($r=-.18$). These measures were moderately reciprocal in the reproductive group ($r=+.33$).

Over 84% of the variation in correlation matrices was shared. ALF rate and nearest neighbor distance were, again, the variables with the strongest mean square correlations in both groups. Frequently used measures of affiliation (neighbor distances, grooming, and ALF rates) were more strongly related than were the affiliative interactions that are more closely associated with sexual interactions (grooming present, present, and mount rates).

Measures of affiliation in the sexually active group were more discordant. In the reproductive group, presents and mounts were reciprocal, whereas they were faintly complementary in the sexually active group.

Male => Male Dyads

There were 6 directional male => male dyads in each group. The matrix correlation was $+.65 (p<.001)$. In the sexually active group, 17 of 21 correlations between measures of affiliation were in the reciprocal direction; in the reproductive group all correlations were reciprocal (Table 4).

Table 4. Male => Male Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		1.00	-.96	-.96	-.97	-.79	-.73	+.23	+.82	-.59
2. Close Neighbor	+.50		-.96	-.96	-.97	-.79	-.73	+.43	+.82	-.39
3. ALF Rate	-.60	-.84		+.89	+.87	+.81	+.75	+.46	+.77	-.30
4. Grooming Rate	-.24	-.48	+.20		+.93	+.84	+.58	+.16	+.75	-.59
5. Grooming Present Rate	+.00	+.00	+.34	-.85		+.65	+.74	+.04	+.74	-.70
6. Present Rate	-.60	-.84	+.77	+.77	-.34		+.37	+.47	+.53	-.06
7. Mount Rate	-.61	-.85	+.99	+.17	+.34	+.75		+.46	+.44	+.02

The coefficient of concordance was stronger in the reproductive group ($W=.84$, $p<.001$) than in the sexually active group ($W=.51$, $P=.003$). There were stronger mean squared correlations in the reproductive group for all variables except mount rate. The correlation between grooming and grooming present rates differed most between groups. Grooming and grooming presents were complementary in the sexually active group ($r=-.34$) whereas they were reciprocal in the reproductive group ($r=+.65$).

Intrasexual competition (Wilson, 1975) between males in the sexually active group over access to the females seems likely to have been expressed by their less reciprocal affiliative interactions. For example, the more a male solicited grooming from another the less likely he was to groom the other male. Analyses were not conducted solely on the dyads composed of sexually mature males since there were only two of these directional dyads in each group.

Female => Female Dyads

There were 56 directional female => female dyads in each group. The matrix correlation for these was positive and significant ($+.90$, $p<.001$). Nineteen of the 21 correlations in the sexually active group were in the expected reciprocal direction; in the reproductive group all correlations were reciprocal (Table 5). The coefficients of concordance were nearly identical in the two groups (sexually active $W=.48$, $p<.001$; reproductive $W=.49$, $p<.001$).

Nearest neighbor distance, close neighbor distance, ALF rate, and

Table 5. Female => Female Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		+.64	-.76	-.66	-.43	-.26	-.07	+.35	+.28	+.07
2. Close Neighbor	+.85		-.47	-.52	-.47	-.26	-.13	+.33	+.20	+.12
3. ALF Rate	-.73	-.72		+.64	+.42	+.44	+.32	+.30	+.28	+.02
4. Grooming Rate	-.78	-.71	+.64		+.10	+.39	+.12	+.29	+.22	+.07
5. Grooming Present Rate	-.17	-.14	+.22	+.00		+.30	+.32	+.07	+.13	-.06
6. Present Rate	-.44	-.42	+.46	+.45	-.01		+.79	+.14	+.20	-.06
7. Mount Rate	-.15	-.15	+.28	-.00	+.58	+.21		+.08	+.15	-.06

grooming rate had stronger mean squared correlations in the sexually active group; the opposite was true for grooming present, present, and mount rates. The correlation between present and mount rates differed most between groups. In the reproductive group presents and mounts were more strongly reciprocal.

In the sexually active group there was less reciprocity in some affiliative behavioral patterns. This may be the result of their more frequent use in complementary and status-related interactions.

Mature Female => Mature Female Dyads

Separate analyses could be conducted on mature female => mature female interactions since there were 20 of these directional dyads in each group. The matrix correlation was +.75 ($p<.001$). Fifteen of 21 correlations in the sexually active group were in the expected reciprocal direction; all correlations in the reproductive group were reciprocal (Table 6). The coefficient of concordance between dyadic values of variables in the sexually active group was .36 ($p<.001$), and coefficient in the reproductive group was a stronger .55 ($p<.001$).

All variables, except close neighbor distance, had larger mean squared correlations in the reproductive group. The correlation between present and mount rates again differed most between groups. In the reproductive group presents and mounts were reciprocal ($r=+.44$). In the sexually active group they were complementary ($r=-.42$).

The matrix correlation was smaller in magnitude than it was for all female => female dyads. The coefficient of concordance of the variables

Table 6. Mature Female => Mature Female Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		+ .54	-.94	-.70	-.34	-.73	-.44	+ .30	+ .42	-.12
2. Close Neighbor	+ .79		-.42	-.67	-.61	-.28	-.24	+ .32	+ .24	+ .08
3. ALF Rate	-.74	-.76		+ .61	+ .33	+ .61	+ .34	+ .23	+ .34	-.11
4. Grooming Rate	-.64	-.76	+ .49		+ .20	+ .66	+ .19	+ .24	+ .30	-.07
5. Grooming Present Rate	-.30	-.26	+ .06	+ .09		+ .09	+ .47	+ .05	+ .15	-.10
6. Present Rate	-.33	-.29	+ .14	+ .46	-.52		+ .44	+ .07	+ .27	-.20
7. Mount Rate	+ .05	+ .03	-.05	-.12	+ .36	-.42		+ .02	+ .14	-.11

variables in the sexually active group was considerably less than between all female => female dyads in that group. Competition between adult females in the in the sexually active group (Michael & Zumpe, 1984) seems a probable cause of the lower concordance of variables and the smaller mean squared correlations for six of the seven variables.

There were negative correlations between several affiliative variables for the females in the sexually active group. In this group, for example, the more mature female "A" mounted mature female "B", the less she tended to groom, present, approach, leave or follow "B". The complementary relationships between the variables may be due to their differential use as a function of status.

Male <=> Female Dyads

There were 48 directional dyads composed of male => female and female => male interactions in each group. The matrix correlation for these interactions was +.97 ($p < .001$). In both groups all correlations were in the expected reciprocal direction (Table 7). The coefficients of concordance in the groups were nearly identical (sexually active group $W = .53$, $p < .001$; reproductive group $W = .55$, $p < .001$).

Four of the mean squared correlations were larger in the reproductive group, 2 were larger in the sexually active group, and the mean squared correlation for grooming present rate was the same in both groups. The correlation between grooming present and present rates differed most between groups; grooming presents and presents were more strongly reciprocal in the reproductive group.

Table 7. Male <=> Female Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		+.72	-.93	-.83	-.39	-.39	-.33	+.36	+.41	-.05
2. Close Neighbor	+.83		-.65	-.57	-.21	-.21	-.15	+.27	+.23	+.04
3. ALF Rate	-.81	-.66		+.84	+.46	+.49	+.39	+.38	+.43	-.05
4. Grooming Rate	-.60	-.57	+.67		+.36	+.49	+.32	+.26	+.37	-.11
5. Grooming Present Rate	-.38	-.17	+.58	+.42		+.62	+.42	+.18	+.18	+.00
6. Present Rate	-.45	-.33	+.39	+.48	+.35		+.29	+.14	+.19	-.05
7. Mount Rate	-.36	-.22	+.49	+.09	+.56	+.14		+.13	+.11	+.02

There was little difference between groups for male <=> female interactions: The matrix correlation was strong, the coefficients of concordance were nearly identical, and there was no strong trend in the differences of the mean squared correlations.

Male => Female Dyads

There was a positive and significant matrix correlation for the 24 male => female directional dyads ($r=+.93$; $p<.001$). In both groups all correlations were in the expected reciprocal direction (Table 8). The coefficients of concordance in the groups were significant and nearly identical (sexually active $W=.56$, $p<.001$; reproductive $W=.55$, $p<.001$).

Five of the seven variables had larger mean squared correlations in the sexually active than in the reproductive group. The mean squared correlation for present rate differed most between groups: it was stronger in the reproductive group. The correlation between nearest neighbor distance and grooming presents differed most between groups: in the sexually active group it was $-.59$; whereas in the reproductive group it was $-.19$.

Male => female interactions also differed little between groups: The matrices were strongly and positively correlated and the coefficients of concordance were nearly identical. There was, however, a tendency toward greater reciprocity of male => female affiliative interactions in the sexually active group.

Table 8. Male => Female Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		+ .64	- .85	- .52	- .19	- .19	- .50	+ .36	+ .29	+ .08
2. Close Neighbor	+ .70		- .66	- .56	- .17	- .13	- .14	+ .22	+ .20	+ .02
3. ALF Rate	- .82	- .67		+ .78	+ .39	+ .35	+ .58	+ .43	+ .40	+ .03
4. Grooming Rate	- .49	- .41	+ .65		+ .26	+ .40	+ .47	+ .22	+ .27	- .05
5. Grooming Present Rate	- .59	- .13	+ .63	+ .55		+ .71	+ .27	+ .27	+ .14	+ .13
6. Present Rate	- .32	- .14	+ .26	+ .08	+ .47		+ .57	+ .10	+ .19	- .10
7. Mount Rate	- .57	- .43	+ .75	+ .46	+ .58	+ .40		+ .29	+ .20	+ .09

Mature Male => Mature Female Dyads

The matrix correlation for the 10 mature male => mature female directional dyads in each group was +.78 ($p<.001$). In the sexually active group all 21 correlations were in the expected reciprocal direction; whereas 18 were in this direction in the reproductive group. There was a strong coefficient of concordance in the sexually active group ($W=.71$, $p<.001$) and a weaker coefficient of concordance in the reproductive group ($W=.49$, $p<.003$).

Every variable in the sexually active group had a larger mean squared correlation. The correlation between grooming and grooming present rates differed most between groups: Sexually active males had a strong tendency to groom present most frequently to the females who they also groomed most frequently ($r=+.82$). There was a faint tendency in the opposite direction in the reproductive group ($r=-.15$).

Greater differences appear between groups for adult male => female interactions. The matrix correlation was lower in magnitude. There were more reciprocal correlations in the sexually active group. The concordance of variables was much stronger in the sexually active group. And every variable in the sexually active group had a stronger mean squared correlation than in the reproductive group.

The greater reciprocity and consistency of affiliative interactions directed by mature males to mature females in the sexually active group may be due to the affiliative interactions between consort pairs. There was, for example, a strong positive tendency for the sexually active

Table 9. Mature Male => Mature Female Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		+ .69	-.79	-.62	+.12	-.33	-.68	+.53	+.34	+.18
2. Close Neighbor	+.74		-.61	-.46	+.20	-.13	-.34	+.32	+.20	+.12
3. ALF Rate	-.90	-.57		+.87	+.05	+.52	+.79	+.63	+.44	+.19
4. Grooming Rate	-.73	-.62	+.78		-.15	+.38	+.90	+.51	+.39	+.13
5. Grooming Present Rate	-.81	-.38	+.95	+.82		+.48	+.02	+.55	+.05	+.50
6. Present Rate	-.41	-.39	+.66	+.69	+.62		+.61	+.34	+.19	+.15
7. Mount Rate	-.69	-.60	+.85	+.64	+.73	+.64		+.49	+.40	+.09

males to grooming present at higher rates to the females they groomed at highest rates. There was a faint tendency for these behavioral patterns to be complementary in the reproductive group.

Female => Male Dyads

The matrix correlation for the 24 female => male directional dyads was +.97 ($p<.001$). In the sexually active group, 20 of the 21 correlations were in the expected reciprocal direction; in the reproductive group all correlations were in this direction (Table 10). The coefficients of concordance were similar in the two groups (sexually active group $W=.54$, $p<.001$; reproductive group $W=.58$, $p<.001$).

Four of the 7 mean squared correlations were larger in the reproductive group. The correlation between grooming and mount rates differed most between groups. There was a weak tendency for reproductive females to have higher rates of grooming with the males who they mounted at higher rates whereas there was no tendency in this direction in the sexually active group.

The interrelationships between the variables in the two groups were nearly identical for female => male interactions since the matrix correlation approached +1.0.

Mature Female => Mature Male

The matrix correlation of mature female => mature male interactions among the 10 directional dyads was +.93 ($p<.001$). In both groups all 21

Table 10. Female => Male Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		+.64	-.86	-.85	-.25	-.60	-.11	+.39	+.38	+.01
2. Close Neighbor	+.70		-.60	-.60	-.28	-.31	-.14	+.24	+.22	+.02
3. ALF Rate	-.88	-.55		+.93	+.49	+.64	+.25	+.36	+.44	-.08
4. Grooming Rate	-.74	-.54	+.73		+.44	+.61	+.24	+.34	+.43	-.09
5. Grooming Present Rate	-.34	-.02	+.45	+.27		+.47	+.65	+.13	+.20	-.07
6. Present Rate	-.64	-.57	+.52	+.78	+.32		+.26	+.29	+.26	+.04
7. Mount Rate	-.18	-.11	+.33	-.03	+.53	+.15		+.08	+.11	-.03

correlations were in the expected reciprocal direction (Table 11). The coefficient of concordance was larger in the sexually active group ($W=.67, p<.001$) than in the reproductive group ($W=.60, p<.001$).

The mean squared correlations were larger for 4 of the 7 variables in the sexually active group, and the mean squared correlation for grooming rate was identical in the two groups. The mean squared correlation for females' rate of mounting males was much larger in the sexually active group. The correlation between present and mount rates differed most between groups: There was a stronger tendency for sexually active females to have higher rates of mounting of the males to whom they presented at highest rates.

Although of lesser magnitude, the differences between groups in mature female => mature male affiliative behavior were in the same direction as those for mature male => mature female affiliative behavior. The variables were more concordant in the sexually active group and 4 of the mean squared correlations were larger in the sexually active group. Mature female => mature male affiliative interactions were therefore more reciprocal in the sexually active group.

The greatest difference between groups was the stronger tendency for sexually active females to mount the males at higher rates to whom they presented at higher rates. Female mounts of males have seldom been analyzed in the literature, yet this infrequent behavioral pattern may be an important component of sexual interactions in rhesus. While further research is necessary, female mounts of males, like threatening away (Zumpe & Michael, 1970), appear to be strong indicators of female proception. The stronger association between sexually active females'

Table 11. Mature Female => Mature Male Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr ²	Rr ²	Diff
1. Nearest Neighbor		+.69	-.77	-.78	-.31	-.74	-.01	+.44	+.39	+.05
2. Close Neighbor	+.74		-.48	-.55	-.41	-.51	-.01	+.33	+.24	+.09
3. ALF Rate	-.94	-.66		+.96	+.60	+.76	+.18	+.52	+.45	+.07
4. Grooming Rate	-.89	-.64	+.84		+.73	+.88	+.31	+.54	+.54	+.00
5. Grooming Present Rate	-.40	-.27	+.51	+.54		+.76	+.45	+.28	+.32	-.05
6. Present Rate	-.69	-.56	+.62	+.88	+.51		+.33	+.42	+.47	-.05
7. Mount Rate	-.57	-.44	+.65	+.55	+.78	+.54		+.36	+.07	+.28

mounts of males, and their presents to those males, may therefore be the result of the greater use of both behavioral patterns in sexual interactions.

DISCUSSION

The positive and significant matrix correlations and coefficients of concordance for every dyad type in both groups were striking results (Table 12). The significant matrix correlations show the measures of affiliation were related in similar ways across the social contexts of the two groups. The significant coefficients of concordance indicate the measures of affiliation tend to assess similar aspects of behavior within groups across the 10 dyad types. These results suggest (1) that affiliation is a useful intervening variable and (2) that the measures used here do assess affiliation.

The matrix correlations, the number of correlations in the expected reciprocal direction, the coefficients of concordance, and differences between groups varied with social context. The utility of measures for the assessment of affiliation was thus partially contingent on who was interacting with whom and the group in which the interactions occurred.

Matrix Correlations

There were three dyad categories for which the matrix correlations were less than +.90 (Table 13). The smallest matrix correlation was for

Table 12. Summary of Variables Used to Describe the Interrelationships between Affiliative Measures for each Dyad Type.

Reciprocal shows the number of correlation coefficients in the expected reciprocal direction; S, Sexually Active Group; R, Reproductive Group; * indicates statistical significance at $p < .05$.

Dyad Type	N of Dyads per group	Matrix Correlation	W Concordance			# Reciprocal	
			R	S	R-S	R	S
all	110	+.95*	+.55*	+.50*	.05	21	21
all sexually mature	42	+.92*	+.55*	+.45*	.10	21	19
all male => male	6	+.65*	+.84*	+.51*	.33	21	17
all female => female	56	+.90*	+.49*	+.48*	.01	21	19
mature female => female	20	+.75*	+.55*	+.36*	.19	21	16
male <=> female	48	+.97*	+.55*	+.53*	.02	21	21
male => female	24	+.93*	+.55*	+.56*	-.01	21	21
mature male => female	10	+.78*	+.49*	+.71*	-.22	18	21
female => male	24	+.97*	+.58*	+.54*	.04	21	20
mature female => male	10	+.93*	+.60*	+.67*	-.07	21	21

male => male dyads, the next smallest was for mature female => mature female dyads, and the third smallest was for mature male => mature female dyads. Contextual differences between groups therefore had the greatest influence on the variables' interrelationships for intrasexual interactions and on interactions directed by mature males to females.

Greater intrasexual competition in the sexually active group seems a probable cause of the smaller matrix correlations for male => male and mature female => mature female interactions. The measures of affiliation were less reciprocal and more complementary in the sexually active group. For example, the greater use of presents between males for appeasement in the sexually active group appeared responsible for the complementary relationship between male => male grooming presents and presents. Males of higher rank solicited grooming with grooming presents and were presented to by the males from whom they solicited grooming. In contrast, male => male grooming presents and presents were strongly reciprocal in the reproductive group.

Mature male => mature female interactions had the third lowest

Table 13. Matrices of the Coefficients of Variation of the Correlation Coefficients across the Interaction Categories Listed in Tables 3-12. Upper Half Matrix: Reproductive Group (R); Lower Half Matrix: Sexually Active Group (S); SCV RCV: The mean squared coefficient of variation for all correlations with the variable in each row for the Sexually Active (S) and the Reproductive Groups (R).

	NN	CN	ALF	GR	GP	PR	MT	SCV	RCV*
1. Nearest Neighbor		+ .17	-.08	-.17	-.76	-.43	-.73	+ .17	+ .23
2. Close Neighbor	+ .14		-.24	-.22	-.80	-.62	-.92	+ .28	+ .34
3. ALF Rate	-.12	-.14		+ .14	+ .46	+ .25	+ .52	+ .16	+ .10
4. Grooming Rate	-.28	-.18	+ .28		+ .88	+ .32	+ .68	+ 1.05	+ .24
5. Grooming Present Rate	-.61	-.71	+ .54	1.96		+ .43	+ .56	+ 2.12	+ .45
6. Present Rate	-.27	-.47	+ .42	+ .41	2.76		+ .38	+ 1.74	+ .18
7. Mount Rate	-.68	-.93	+ .62	1.44	+ .26	1.48		+ 1.01	+ .43

matrix correlation. This was the result of the greater reciprocity of these interactions in the sexually active group. Sexually active adult males had, for example, a strong tendency to groom most with the adult females to whom they also most frequently grooming presented. There was a faint tendency in the opposite direction in the reproductive group. The greater reciprocity of mature male => mature female interactions in the sexually active group seems likely to be the result of the affiliative interactions occurring between sexually interacting pairs and the more solicitous and tolerant behavior (Carpenter, 1942b) of the males in those pairs.

Coefficients of Concordance

Male => male interactions had the greatest difference in coefficients of concordance, mature male => mature female interactions had the second greatest, and the third greatest difference was in mature female => mature female interactions. These are the three dyad types that had the smallest matrix correlations.

Two of the three greatest differences in the coefficient of concordance arose for intrasexual interactions. Intrasexual competition associated with higher rates of sexual behavior is, again, the probable cause of the lower concordance between affiliative variables in the sexually active group. Decreased reciprocity of intrasexual interactions

in the sexually active group may be a form of intrasexual competition: One individual in the dyad receives decreased social resources compared to the other. If, for example, a male in the sexually active group more frequently presented for grooming to another male he was less likely to groom that male.

Discordance between measures of affiliation suggests social signals might sometimes be inconsistent, an inconsistency that could be an indirect measure of deception (Byrne & Whiten, 1988). For intrasexual interactions in the sexually active group, patterns of affiliation as assessed by one variable tended to be much less predictive of affiliation as measured by the other variables. In the sexually active group, for example, a strong tendency for male "A" to be a close neighbor to "B" had no covariation with rate at which male "A" grooming presented to "B" ($r=0$). In the reproductive group these two variables were almost perfectly related ($r=-.97$).

The second greatest difference in the coefficients of concordance between groups was for mature male => mature female interactions. There was a much stronger coefficient of concordance in the sexually active group. The greater reciprocity of mature male => mature female interactions in the sexually active group appeared to cause the difference in the coefficients of concordance between the two groups.

Number of Correlations in the Expected Reciprocal Direction

The number of correlations in the expected reciprocal direction differed across groups and interaction categories (Table 12). In the reproductive group 9 of the 10 interaction categories had all 21 correlations between the measures of affiliation in the expected reciprocal direction. In the sexually active group only half the interaction categories had all correlations in this direction. Interactions were therefore more consistently reciprocal in the reproductive group than in the sexually active group. The only deviation from the trend was for mature male => mature female interactions. For these, all correlations were in the expected reciprocal direction in the sexually active group whereas 18 of 21 were in this direction in the reproductive group.

Variability of the Correlations between Affiliative Variables

There was variation in the sign and magnitude of the correlations between measures of affiliation across interaction categories. This variation between groups and across the 10 dyad categories was measured with coefficients of variation. These were calculated for each of the 21 correlation coefficients across the 10 dyad types (Table 13).

The coefficients of variation were larger and more varied in the sexually active group (mean $=+.28$, $SD=.95$) than in the reproductive group (mean $=-.01$, $SD=.54$). Correlations with grooming presents had the largest mean squared coefficient of variation across dyad types in both groups. Grooming presents were therefore the measure of affiliation most sensitive to dyad type.

In the sexually active group the correlation between grooming presents and presents varied most across dyad types ($CV=2.76$). This correlation was large and negative for the mature female \Rightarrow mature female and male \Rightarrow male interactions. The correlation was large and positive for the mature female \Rightarrow mature male and the mature male \Rightarrow mature female interactions. The magnitude of variation in this correlation across dyad categories was the result of the complementary use of grooming presents and presents in intrasexual interactions and their reciprocal use in the heterosexual interactions.

In the reproductive group the correlation between grooming and grooming presents was also most varied across dyad types. Exactly opposite to the sexually active group, this correlation was smallest and negative for mature male \Rightarrow mature female interactions and reached its largest positive value for male \Rightarrow male interactions. This contrast between groups may be the result of more status related, and less sexual, heterosexual affiliative interactions between adults and the less competitive interactions between males in the reproductive group.

CONCLUSION

Nearest and close neighbor distances and ALF rate tended to be most strongly correlated with the other measures of affiliation; these might therefore be considered the most general measures of affiliation. These measures also varied least across dyad types and differed least between groups. These measures might therefore be those most appropriate for comparisons of affiliative tendencies across dyad types and social contexts. This result supports Carpenter's belief (1942a) that the strength of attachment between two individuals could be measured by the average distance separating the two animals.

There was variation in the relationships between the measures of affiliation within and between groups across dyad types. If the variables are "measuring sticks" of affiliation their length is not constant. The social context and the dyad types must therefore be considered for an accurate assessment of the affiliative relationships between individuals and the meaning of these affiliative relationships.

The differential concordance of the measures of affiliation suggests

that overlapping sources of information could be used by monkeys to both signal their affiliative tendencies toward each other and interpret the affiliative interactions that they receive. We tend to feel more confident say, that another person means yes when they nod yes, say yes and write yes. When a person nods yes, says yes and writes no, then meaning becomes more difficult to interpret and we may suspect deception.

The analyses presented here only provide an initial step toward the assessment of the utility of affiliation as an intervening variable. Further analyses are necessary to determine how these measures are associated with unambiguously sexual or agonistic interactions. Analyses are also necessary on the use of affiliative interactions, such as grooming presents, in status interactions. When affiliative interactions are used in status interactions they may simultaneously convey both agonistic and affiliative information.

Evolutionary theory is the unifying theory by which we determine the functional significance of behavior, the way in which the behavior is associated with fitness (Tinbergen, 1965; Wilson, 1975; Rasmussen, 1988). Intervening variables used in studies of behavior should therefore be useful for understanding fitness (Brown, 1983). There has, for example, been considerable attention devoted to the links between dominance and aspects of fitness (Cowlishaw & Dunbar, 1991). Analyses must also be made of the relationships between affiliative interactions and increments or decrements in fitness.

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APPENDIX

Neighbor Distances

The coded distance of the focal subject to the nearest male and the nearest female was instantaneously sampled at the beginning of each 2 min interval (codes: contact=0, not touching to 1/3 m=1, 1/3-2/3 m=2, 2/3-1 m=3, 1-4/3 m=4, 4/3-5/3 m=5, 5/3-2m=6, greater than 2 m=7). When individuals were engaged in agonistic behavior with the focal subject they were excluded as nearest neighbors since neighbor distances were used to assess affiliation (Rasmussen, 1984). On the rare occasions when two or more individuals of the same sex were exactly the same distance to the focal subject, the individual chosen as the nearest neighbor was determined by application of 3 successive decision rules: First, the neighbor who was near the focal subject for the longest duration of time was scored as the nearest neighbor. Second, if the neighbors had been close to the focal subject for an equal amount of time, the one who was either grooming, or who was being groomed, by the focal subject was scored as the nearest neighbor. Third, if the neighbors were close to the focal subject for an equal time and engaged in grooming

with the focal subject, the individual chosen as the nearest neighbor was the one who had the greatest amount of body contact with the focal subject.

Two types of mean distance between dyads were calculated: First, the mean ordinal distance across all focal samples, nearest neighbor distance. Second, the mean distance during only those intervals when dyad members were separated by 2 m or less, close neighbor distance (Rasmussen, 1983). Nearest neighbor (NN) distance was the sum of coded distances between dyad members divided by all focal two min intervals collected on the dyad. When the focal subject had a nearest neighbor all other group members of the same gender as the nearest neighbor were given a coded distance of 7 from the focal subject for that 2 min interval. Close distance (CD) was sum of coded distances between a dyad, excluding code 7, divided by all 2 min samples on the dyad when they were nearest neighbors and within 2 m.

ALF - Approach, Leave and Follow

"A" was scored as approaching another "B" when it approached within 1 m of "B", and remained within 1 m for at least 15 sec. When several animals were approached, the approach was scored only for the animal most closely approached. A leave was scored when "A" walked at least 1 m away from "B" who had been its nearest neighbor and separated by no more than 1 m for at least 15 sec. "A" was scored as following "B" when it walked at 1 m or less behind "B" over a distance of at least 1 m. Since approaches, leaves and follows were used to assess affiliation, these variables were not scored if they were part of an agonistic interaction with the focal subject. Approach, leave and follow rates were calculated as the sum frequency of each variable divided by all 2 min samples collected on the dyad members. The rate at which the oldest male approached the oldest female was, for example, the number of times the male approached the female divided by all 2 min samples collected on the male and female.

The Pearson correlation between approach and follow rates across all directional dyads in both groups (N=220) was +.80; the correlation between approach and leave rate was +.87; and the correlation between leave and follow rate was +.66. Because of their strong correlations, the three variables were combined in a composite variable called ALF rate: the sum frequency of the variables divided by all 2 min focal sample intervals collected on both dyad members.

Grooming

Picking through the hair or skin of another with fingers or teeth was defined as grooming (e.g. Cullen 1963; Sade, 1965; Sparks, 1969; Rasmussen, 1984). The beginning and end of grooming bouts were difficult to accurately record because many variables were used to assess group social organization. Grooming was therefore assessed with 1/0 sampling. 1/0 grooming rate per 2 min interval was calculated as the sum of intervals one group member was observed to groom another divided by all 2 min intervals collected on the group.

Grooming Presents

"A" grooming presented (Boccia et al., 1982) to "B" when it approached and exposed a body part at 1/3 m or less to "B's" hands or mouth. Sometimes an individual presented the genital area for grooming. When this happened a grooming present was distinguished from a present by (1) the lowering of the head and shoulders below

horizontal, often so that the head touched the floor, and (2) by the animal who received the grooming present responding by grooming. "A" => "B" grooming present rate was calculated by dividing all grooming presents of "A" => "B" by the sum of focal 2 min intervals on "A" and "B".

Presents

"A" presented to "B" when it was within 2 m of "B" and oriented its anogenital region to "B's" face. Present rate was calculated by dividing all "A" => "B" presents by the sum of focal 2 min intervals collected on "A" and "B".

Mounts

"A" mounted "B" when it placed both hands on "B's" back and the anogenital regions of the two were aligned in a copulatory posture. Mount rate was calculated by dividing the sum of "A" => "B" mounts by the sum of all 2 min intervals collected on their group.

USE OF AN EGOCENTRIC FRAME OF REFERENCE BY GROUPED FISH (*Aphyocharax erithrurus*) IN A SPATIAL DISCRIMINATION

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ABSTRACT: Small groups of fish of a schooling species (*Aphyocharax erithrurus*) were trained to turn right or left in order to avoid being temporarily swept out of the water. This was achieved by a rotating avoidance paddle approaching them with one door (right or left) open. Once a learning criterion was attained, the direction of the paddle was reversed and both doors were opened. During these inversion trials, fish chose the door which was at the same side in relation to their body, showing that egocentric clues were used when facing the problem from an opposite viewpoint. When vertical black and white stripes were present at one side of the tank, a different response appeared during the inversion trials: fish passed through the door nearest to the stripes regardless of which door was open during training. It is concluded that these fish use egocentric references when the spatial problem is reversed by 180°, and that this response is overridden by a tendency to swim near a vertically striped background.

INTRODUCTION

Spatial orientation of animals and humans may be based on a reference system centred on their own body (egocentric orientation) or may rely on environmental stimuli (allocentric orientation) such as sun, stars, landmarks, odours or geomagnetic clues. Landmarks may be used simply as corrective feedback clues to orient movements by approaching it, avoiding it or maintaining a constant angle to it while travelling (Etienne et al., 1990b; Morris, 1981; Collet, 1987). But several landmarks may be taken together so that relational information may be used to construct a spatial representation or map (O'Keefe & Nadel, 1978; Nadel, 1990). This enables the subject to direct its movements to

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a particular place, even when approaching it from an unfamiliar viewpoint.

An experimental strategy used to discover the reference system in which spatial relations are punctuated while a subject contacts the environment, is to probe its response in different, altered ways after a learned spatial task has been solved (Nadel, 1990). One procedure is to compare the path during the outward and returning journey of a homing animal. Using this approach, gerbils appear to use an external or allocentric frame of reference to solve a spatial memory task (Thinus-Blanc & Ingle, 1985). Dogs trained in a "returning" task, initially base their orientation on a variety of external clues. But once criterion is reached, kinaesthetic (egocentric) clues predominate (Chapuis & Melin, 1979).

Other authors tested the spatial system of their subjects by introducing them into the experimental arena from a viewpoint different to the one available during learning (Acredolo, 1978; Thinus-Blanc & Ingle, 1985; Thinus-Blanc, Durup & Poucet, 1992). For instance, Acredolo (1978) found that after being rotated by 180° , spatial orientation in 6-months and 11-months-old children depends on an egocentric frame of reference when discriminating locations of objects within a familiar arena. In contrast, 16-months-old infants are able to keep track of their movements in space, showing an allocentric (objective) rule of orientation. The presence of a landmark did not change this situation. An objection to this changing viewpoint technique is that uncontrolled stimulation (internal and external) may occur during the passive relocation of the subject.

Fishes represent a low evolutionary stage of living vertebrates. Thus, the evaluation of their behavioural competence is interesting for comparative studies. Many studies have been performed on how fish handle space in large (Smith, 1985) and medium scale (Levin et al., 1989) migrations, but little is known about their ability for solving particular spatial discrimination problems. Several years ago, we designed and used the avoidance paddle to train fish on spatial discrimination problems. This technique is a one-way alternative to the shuttle-box that produces a large increase in the rate of spatial discriminated avoidance behaviour (Levin et al., 1982). This technique was used to compare the performance of individuals and groups in a spatial reversal learning task. The outcome was that only groups improved along reversals (Levin & Vergara, 1987). The avoidance paddle direction of rotation may be inverted at any time during training without changing any other aspect of the situation, and without manipulating the subject between trials. Thus, it offers a good method to study the reference system in which spatial responses are learned.

The purpose of the present experiment was to establish the spatial relationships that occur when groups of schooling fish are confronted with a 180° reversal of a learned spatial discrimination. This is evaluated in absence or in presence of external conspicuous references. Since our experimental subjects are extremely social because they are obligate schoolers (Shaw, 1970; Smith, 1985), small groups rather than individuals were used as experimental units.

METHODS

Subjects

Sixteen *Aphyocharax erithrurus* (Teleostei: Characidae) "rubicandela" ranging from 28 to 33 mm were used in this experiment. The fish were caught in shallow streams at Mantecal, Estado Apure, in Southern Venezuela with a thin mesh net, and were taken to the laboratory in plastic bags where water and oxygen was added. The specimens were kept for about two months before the experiment, in a 40-liter common tank filled with dechlorinated tap water that was maintained at 24°C, and were fed daily with dry food. They were randomly assigned to four groups of four individuals each. Each group was assigned to a different semicircular tank, where training and test trials were conducted.

Apparatus

The experiments were performed with the avoidance paddle, which has been fully described elsewhere (Levin, et al., 1982; Levin & Vergara, 1987). The paddle was a light plastic framework covered by a nylon net, which could be rotated in a semicircular tank (radius of 25 cm, wide of 10 cm) where the fish were kept. The paddle borders accurately adjusted to the tank walls (Fig. 1). The paddle was progressively moved through the water reducing the space where the fish were. The fish could surpass the approaching paddle and escape the space reduction by fleeing through a lateral doorway to avoid being temporarily swept out of the water (an error). The doorways were small corridors (6 x 11 mm) located at the end of two hollow pyramidal funnels placed side-by-side at the paddle extreme. This structure was symmetrically repeated at the opposite side of the paddle, so that its shape was the same regardless of its turning direction. The corridors could be closed with sliding transparent doors. A flat-black partition projected forward in the vertical midline. This barrier made left-right movements of the subjects

difficult while near the paddle. The barrier was opaque because previous observations showed that fish were unable to detour around a transparent partition (Levin, 1986). Thin plastic flappers shielded the space between the paddle and the tank walls.

The passage angle of the group was considered as follows: the curved bottom of the tanks was marked at 10° intervals. When the first fish of the group passed the door, the position of the paddle against the marks was recorded. The angular values increased in the direction of the turning paddle from 10 degrees, where the paddle made contact with the water surface, to 170 degrees where it left the water.

Groups of fish remained in separate semicircular tanks throughout the experimental period. The paddle was placed in each tank when performing each session. Illumination was provided by a 40-W incandescent reflector placed 20 cm above the water level.

For the asymmetric condition, a conspicuous landmark in the panorama was introduced by placing a white card with black 5-mm-wide vertical stripes 10 mm apart, against the glass on the right hand side.

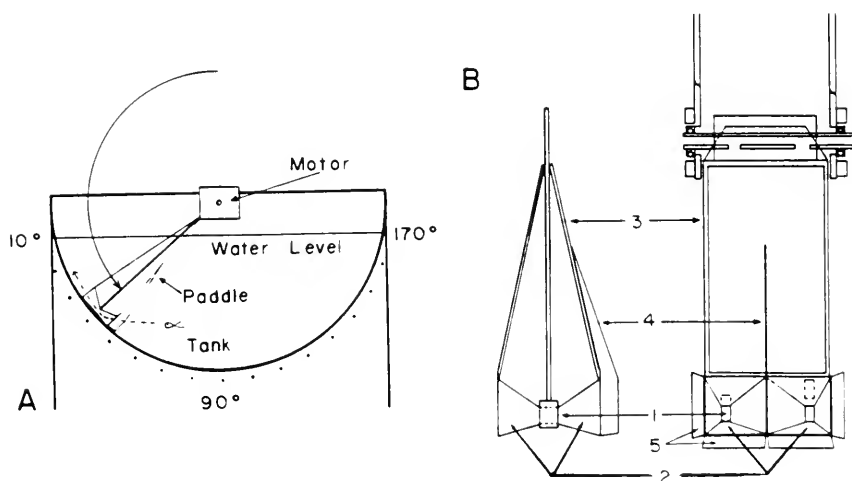


Figure 1. A, Diagram of the avoidance paddle. The paddle sweeps through the semicircular tank, entering the water at 10° and emerging at 170° . Fish may escape the space reduction or avoid an emergence from the water by passing through the open door (dashed line). B, Lateral (left) and frontal (right) view of the turning paddle. 1, funnels; 2, flappers; 3, partition; 4, framework; 5, flappers (modified from Levin et al. 1982).

Procedure

Each trial consisted of a 360° turn of the paddle (one turn in 25 s) starting at a high vertical position. One session per day of 40 trials with an inter-trial interval (ITI) of 30s was administered to each group until the criterion (10 successive trials with no errors) was obtained. Once this criterion was reached, and after the normal ITI, the inversion test was performed. That is, during four trials (inversion trials) the paddle turning direction was reversed and both doors remained open. The same ITI was applied.

Observations were made through a one-way mirror placed at an angle to the tank wall, so that the fish would not see their own reflected image. On each training trial, the number of errors was recorded. During the inversion trials, the number of passages through each door was recorded. The passage angle was also recorded.

The experiment consisted of 4 phases in which the same procedure was followed except that, in phase I, there was a symmetrical panorama: with identical one-way mirrors placed at both sides of the tank (only one was actually used). In phases II and III, a marked asymmetry was introduced into the panorama by placing the vertically striped card against the glass on the right hand side. In phase IV, the striped card was removed. Once again the panorama became symmetrical as in phase I. During phases I and II, training for groups G1 and G2 was performed with the left door open (left or right relative to the fish body when heading towards the approaching paddle), and with the right one open for groups G3 and G4. At the end of phase II, the open door was shifted right-left for the four groups.

Phase I was intended to show how fish orientation was shifted when the spatial problem presentation was rotated by 180°. The effect of strong asymmetrical clues on this transfer was tested in phase II. With the aim of balancing order effects, phases III and IV were performed. At the end of phase II, the open door was shifted right-left, with the striped card remaining at the right side of the tank. Hence, training began "de novo" under asymmetrical conditions.

RESULTS

The number of fish that passed through the door opposite to the training door during the four trials of each inversion test was expressed as the percentage of the total number of passages during the test (%EGO). The %EGO for each successive inversion test was plotted for

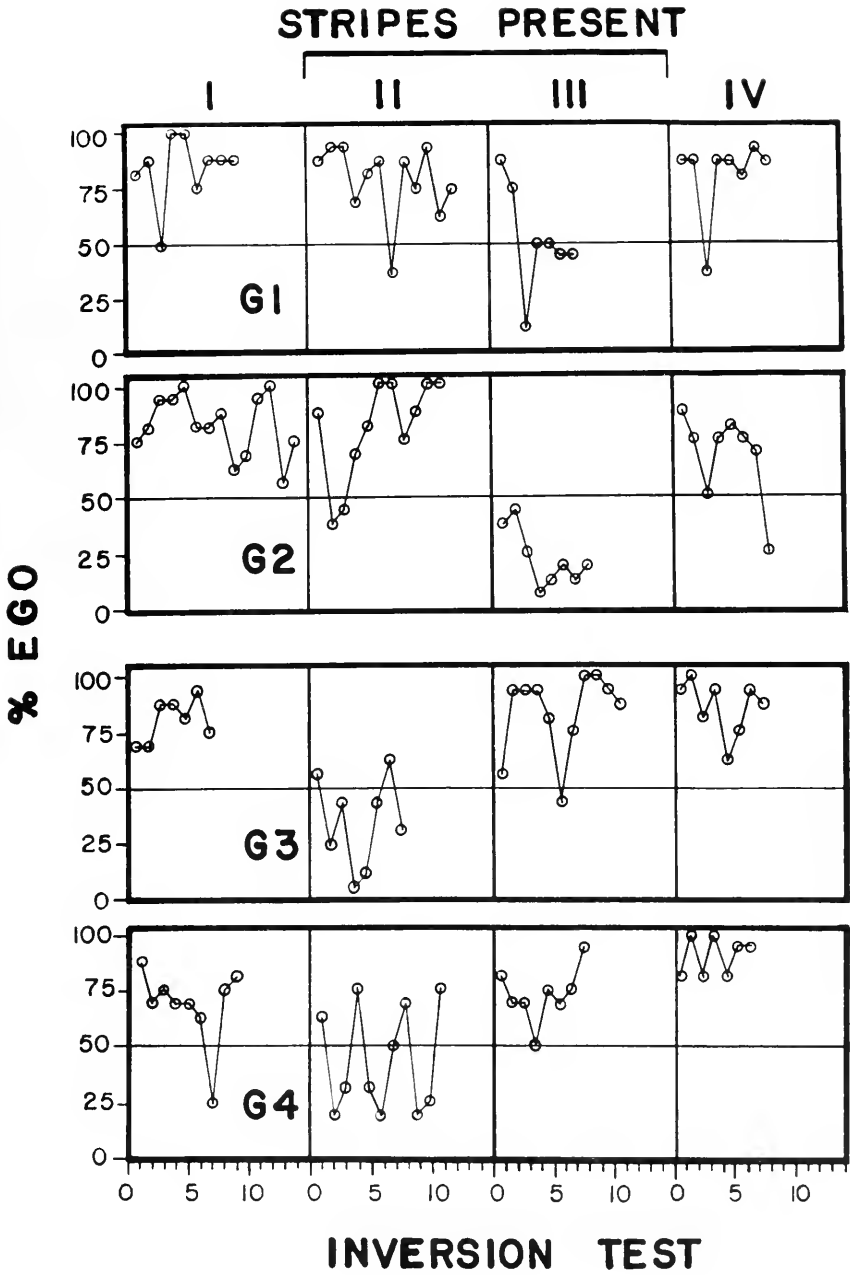


Figure 2. Percentage of individuals which passed through the door opposite to the training one with respect to the number of passages through both doors (%EGO), during each successive inversion trial along the four experimental phases, for groups G1-G4.

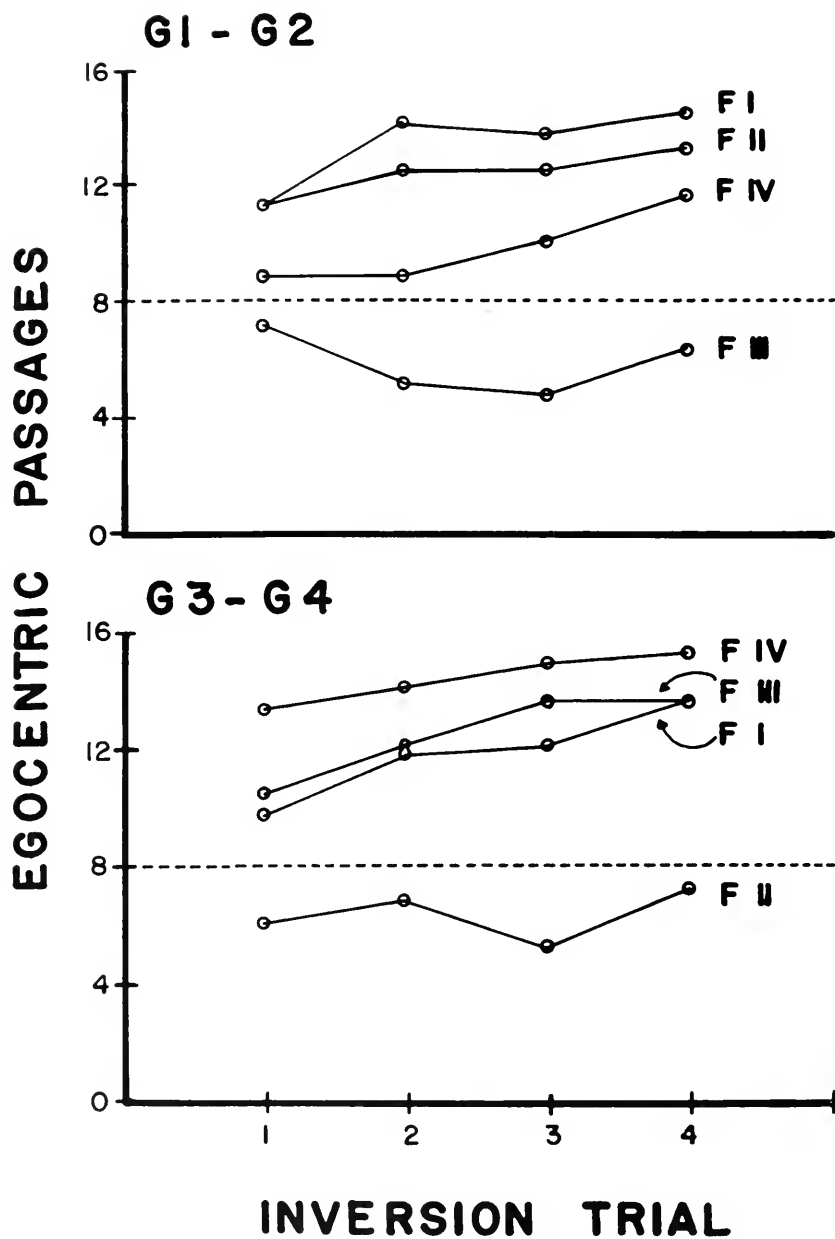


Figure 3. Mean number of fish which passed through the door opposite to the training one during each of the four inversion trials in the four phases (P). Replicate groups (G1-G2 and G3-G4) are pooled together. The horizontal line at 8 indicates an equal number of passages through both doors.

the four groups along the four phases (Fig. 2). During phases I and IV, the %EGO for all the groups were over 50% (binomial test: 68 cases out of 74, $p < .001$). When there were stripes, the outcome was also over 50% but only for groups G1-G2 in phase II (21 out of 23, $p < .001$) and for G3-G4 in phase III (18 out of 19, $p < .001$). On the other hand, groups G1-G2 in phase III were under 50% (11 out of 15, $p \leq .05$) and groups G3-G4 in phase II were not different from 50% (12 out of 19, $p = .1$). Such apparently non-egocentric cases were those in which training proceeded with the door nearer to the stripes open, so that egocentric orientation would result in fish passing at a distance from the stripes during the inversion trials.

Figure 3 shows the number of fish that passed through the door opposite to the training one, during each of the four successive inversion trials in each of the four phases. Replicate groups (G1-G2 and G3-G4) were pooled. It can be seen that, there are two cases in which the plots fall below the horizontal line at 8 (which indicates an equal number of fish by each door). These correspond to phase III for groups G1-G2 and to phase II for groups G3-G4, which are the above mentioned apparently non-egocentric cases. All the other curves are over the horizontal line, and their value increases with trials ($F(3, 20) = 3.40$, $p < .05$).

The passage angles of the four trials immediately before (Mean = 68.4, SD = 4.8), and during (Mean = 93.6, SD = 24) the four inversion test trials, pooled for all the inversion tests, were compared. The "during" angle was larger than the "before" angle (Mann Whitney "U" = 28.5, $p < .01$) ($n = n = 16$). This means that when the paddle turning direction was reversed, the fish passage through the door was delayed, even though, during the test, both doors were open. The difference between the mean passage "during" and "before" angles, was larger when there was a vertically striped card in one side of the tank (phases II and III: 36.3°, SD = 25°) than when it was absent (phases I and IV: 15.3°, SD = 5°; Mann Whitney "U" = 47, $p < .02$, $n = n = 8$).

The number of errors per session during training in phase II for G1-G2 was larger than for G3-G4. During phase III the reverse was true (Kolmogorov-Smirnov, $p < .05$ in both cases).

DISCUSSION

Once a group of fish learnt to swim through one of the lateral doors of the paddle, the reversal of the paddle direction with both doors open provided a test for the frame of references used by fish when facing the problem from the new viewpoint. Without conspicuous landmarks, fish responded egocentrically. That is, they passed through the door located

at the same side in relation to their own body, which is opposite to the one used during training. Mammals respond in a different way in what seems to be a similar situation. Lukaszewska (1961) suggested that the successful return journey made by rats in a T-maze must be based on the reversal of the direction taken on the outward path: a right-hand turn when the outward path involved a left-hand turn and vice-versa. Blind rats perform as well as normal ones indicating that kinaesthetic information is used in this task. Golden hamsters also base their homing trajectory in self-generated, route-based signals collected during their outward path when returning from a feeding place to their nest (Etienne et al., 1985; 1990a). In dogs, returning behaviour can be based upon a wide range of cues early during training but when the problem is mastered, they mainly rely on kinaesthetic cues (Chapuis & Melin, 1979). This kind of "route reversal" homing has been also described in pigeons (Wiltschko & Wiltschko, 1987).

The present results show that, at least when no external cues are present (phases I and IV), the fish do not return using the same route. The opposite door is used, which means that fish adopt a strictly egocentric solution, without correcting their response in accordance with the reversal of the problem. The likelihood that fish did not notice the paddle reversion is ruled out by the significant increase in the delay of the passages (larger passage angle) during the four inversion test trials. This suggests that the fish perceived the reversal direction of the paddle as a novel situation (Missilin & Ropartz, 1981; Save et al., 1992). Mechanical noises and the timing of the experimental events did not change with the change in paddle direction, and no conspicuous asymmetric clues were present. Thus, the change in paddle direction could be only detected by the fish by keeping track of their movements during the ITI, perhaps by kinaesthetic cues (Chapuis, 1982) or inertial integration (Barlow, 1964; Levin et al., 1989; Levin & González, 1994). In fact, when external asymmetric clues were available, an increase in angle retardation was measured during the inversion trials. This indicates that the novelty of the situation was perceived by the fish. In fact, when the inversion test was performed with landmarks present, two dimensions change: the inertial (or kinaesthetic) one, and the landmark side, relative to the responding fish axis. The egocentric tendency increased along the four successive test trials, suggesting that habituation of the disruptive effects of the novel situation had occurred.

However, when asymmetric landmarks were available, egocentric responses appeared only if they corresponded with approaching the stripes (groups G1 and G2 in phase II, and groups G3 and G4 in phase III). When the egocentric response would compel the fish away from the stripes during the test, an opposite reaction appeared: the fish again

passed the door nearest to the stripes (groups G1 and G2 in phase III and groups G3 and G4 in phase II). Two alternative explanations could account for these cases: either an "environmental" or absolute frame of reference is used in orienting the response, or superimposed with egocentricity, there is a tendency to pass the door as near as possible to the stripes. If an environmental rule was the case, groups G1 and G2 in phase II and groups G3 and G4 in phase III should also give an environmental response, which did not occur. Thus, a "visual discontinuity" taxis (Benhamou & Bovet, 1992) is validated. If this taxis is operative during the inversion trials, it should also be present during training. In fact, this was the case. The number of errors were larger when training proceeded through the furthest door rather than through the nearest one to the stripes.

This "visual discontinuity" taxis may be based on an optokinetic response (Bayliss, 1966). The body moves tending to stabilize the stripes in the visual field. This results in a slowing of the side of the fish nearest to the stripes. Thus, the fish turns and reduces the distance to the stripes. This response may have the adaptive advantage of directing the escape reaction towards discontinuities as those offered by the many aquatic reeds and plants that may provide refuge in the natural habitat of this fish. Another freshwater fish *Coreoperca kawamebari* has been found which prefers a vertically striped background rather than a horizontally striped or all white one (Yasutoshi & Watanabe, 1986).

Longitudinal studies of orientation rules in children have shown a shift from (strict) egocentric to an external frame of reference in localizing expected objects (Acredolo, 1978; 1990). Different specialized structures of the brain of mammals are responsible for these different functions (Buzsáki et al., 1982; Nadel, 1990) and they have different ontogenetic timecourses (Acredolo et al., 1975). A general picture of an increasing scale of sophistication and adaptivity has grown from these evidences. Some authors have considered that allocentric orientation involves a more "abstract" function than the apparently more simple egocentric orientation (Thinus-Blanc & Ingle, 1985). O'Keefe and Nadel (1978) considered three different kinds of behavioural strategies or hypothesis: "orientation", based on body-turns, "guidance"; based on individual landmarks; and "place" based on a set of landmarks relationally taken. Our finding of a strict egocentric rule for fish solving a spatial reversal task may suggest that these primitive vertebrates can achieve only the lowest degree of spatial differentiation. However, fish can perform outstanding homing trips of thousands of miles with extraordinary precision (Smith, 1985), where highly sophisticated orientation mechanisms are evident (Northcote, 1984; Levin et al., 1989). Today, there is a growing accumulation of evidence in favour of

the idea that all metazoans possess multiple orientation capabilities which interact hierarchically with one another (Able, 1991). How the egocentric response shown here relates to other orientation mechanisms, needs to be further examined.

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